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Historical niche partitioning and long-term trophic shifts in Laurentian Great Lakes deepwater coregonines

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Abstract. Over the last 100 yr, anthropogenic stressors have decimated the assemblage of deepwater coregonines that once underpinned the food webs of the Laurentian Great Lakes. As a part of ongoing restoration efforts, fisheries managers are interested in reintroducing deepwater coregonines from remnant populations to reestablish historical food web connections. However, little is known about historical trophic position and niche partitioning among deepwater coregonines in the Great Lakes. We used nitrogen stable isotope analysis of amino acids to compare trophic position of museum-preserved (1920s) and present-day forage fishes in Lakes Michigan and Superior. In the 1920s, deepwater coregonines exhibited clear trophic niche partitioning, with trophic positions spanning a full trophic level. Additionally, species trophic positions were tightly conserved between lakes. In Lake Superior, trophic niche partitioning has been maintained over the last 100 yr, but trophic position has shifted downward by ~0.5 trophic level. The more dramatic species loss in Lake Michigan corresponds with a sharp reduction in trophic niche breadth over time. Our study reveals remarkable trophic niche breadth among deepwater coregonines prior to the major anthropogenic impacts on the Laurentian Great Lakes and provides a food web benchmark for restoring the historical trophic diversity of this iconic species flock.

Key words: compound-specific; *Coregonus* species; food webs; Lake Michigan; Lake Superior; museum specimens; niche partitioning; species reintroduction; stable isotopes; trophic compression.

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INTRODUCTION

Human activities have resulted in population declines, local extirpations, and, in many cases, extinction of native species (Dudgeon et al. 2006). A century ago, offshore habitats in the Laurentian Great Lakes were dominated by an assemblage of seven closely related species of deepwater ciscoes (*Coregonus* spp.), comprising a total of 26 lake–species combinations (Eshenroder et al. 2016). Deepwater coregonines were the dominant prey of the native apex predator, lake trout (*Salvelinus namaycush*), and played a crucial role in linking lower and higher trophic level production. By the 1960s, 15 of the 26 deepwater cisco populations had been extirpated from the Great Lakes. Such declines were largely due to commercial harvest and the effects of introduced species, especially sea lamprey (*Petromyzon marinus*; Eshenroder et al. 2016).

Today, all deepwater cisco species except bloater (*Coregonus hoyi*) have been extirpated from Lake Michigan. In contrast, Lake Superior retains the most intact deepwater assemblage of the Great Lakes, with populations of bloater, kiyi (*Coregonus kiyi*), and remnant populations of blackfin cisco (*Coregonus nigripinnis*), shortjaw cisco (*Coregonus zenithicus*), and shortnose cisco (*Coregonus reighardi*; Schmidt et al. 2009). The collapse of deepwater coregonine assemblages has left vast habitats of the Great Lakes depopulated

(Eshenroder and Burnham-Curtis 1999). Non-native fishes such as alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) have generally thrived and have become the dominant prey of lake trout and introduced Pacific salmonids (Bunnell et al. 2014,).

Rehabilitation of native fish assemblages in the Great Lakes is a central goal of fisheries managers, and reintroduction of deepwater coregonines is a major component of this restoration effort. For example, bloaters have been reintroduced into Lake Ontario, and fisheries managers have considered introducing deepwater coregonines from Lake Superior or Nipigon into Lake Michigan (Zimmerman and Krueger 2009). However, it is not known how anthropogenic impacts and species loss over the past century have affected system biostructure (sensu McCann 2007)—the network of interactions among organisms, including food web linkages and pathways of energy flow to higher trophic levels, which ultimately support the provisioning of ecosystem services. We argue that if restoration is to proceed, there is a need to understand historical trophic niche partitioning among species, as well as food web changes resulting from species losses, species invasions, and other human impacts.

Several studies have used stable isotope analysis of archived tissues to quantify long-term food web change (Wainright et al. 1993, Vander Zanden et al. 2003). In the Great Lakes, bulk stable isotope analysis of historical deepwater coregonines from museum collections revealed evidence for trophic niche partitioning (Schmidt et al. 2011). As with other historical food web reconstructions, Schmidt et al. (2011) were not able to establish the historical isotopic baseline (the nitrogen isotope value of primary producers or primary consumers, from which trophic position is calculated using bulk stable isotopes) because organisms used to establish baselines were not part of museum collections. Unknown baseline shifts can obscure food web patterns, or create the appearance of food web shifts where no food web shift occurred. Resolving the isotopic baseline represents a methodological challenge for the application of bulk stable isotopes in food web studies (Cabana and Rasmussen 1996).

Amino acid-specific nitrogen isotope analysis is an emerging approach that may overcome some of the limitations of the bulk stable isotope approach (Chikaraishi et al. 2009). Specific amino acids known as "source" amino acids change little from food resource to consumer, while another group of amino acids referred to as "trophic" amino acids exhibit relatively large and consistent increases in $\delta^{15}N$ from prey to consumer. An organism's trophic position can then be determined by the $\delta^{15}N$ difference between "source" and "trophic" amino acids (Popp et al. 2007, Chikaraishi et al. 2009). The amino acid-specific method has a distinct advantage for studies of historical food webs where the isotopic baseline is lacking or trophic relationships are poorly understood (e.g., where the appropriate baseline organism is unknown). The amino acid-specific approach also provides higher precision and accuracy than bulk methods for estimating consumer trophic position because the $\delta^{15}N$ values of trophic amino acids tend to have a larger and more consistent trophic enrichment than bulk tissue (Chikaraishi et al. 2009, Blanke et al. 2017).

Here, we conduct amino acid-specific isotope analysis on museum-preserved deepwater coregonines from Lake Michigan and Lake Superior. We also analyze present-day forage fishes in these lakes to examine how trophic niche partitioning has changed over the past century. Few studies have used amino acid-specific stable nitrogen isotope analysis to study freshwater food webs (Ogawa et al. 2013, Kruger et al. 2016). Our work highlights the application of this approach for understanding how food web interactions and trophic niche partitioning have changed over time.

Methods

Museum-archived deepwater coregonine specimens captured in Lake Michigan in June–August 1923 and in Lake Superior in September and October 1923 (with the exception of Lake Superior *Coregonus kiyi*, captured in July and December, 1922) were chosen to examine the historical trophic niche partitioning of the deepwater coregonine species as described in Koelz (1929). We chose adults of similar size for each species–lake combination. All individuals were captured in the same region of each lake (the eastern region of Lake Michigan and the northwest region of Lake Superior). We also analyzed gut contents from the stomachs of two historical *Coregonus reighardi* specimens from Lake Michigan, which consisted entirely of *Mysis*

diluviana, to calculate historical *Mysis* trophic position. To prepare the historical deepwater coregonine samples for bulk and amino acid-specific and nitrogen isotope analysis, dorsal muscle samples were ground to a powder after drying for 24–48 h at approximately 60°C.

Formalin tissue preservation and ethanol tissue preservation have been shown to have minimal overall effect on bulk $\delta^{15}N$ (Arrington and Winemiller 2002, Sarakinos et al. 2002). Moreover, two recent studies have demonstrated no effect of formalin preservation on amino acid-specific nitrogen isotope values (Hannides et al. 2009, Ogawa et al. 2013). An assumption of our study is that the lack of preservation effect observed over short time periods applies to much longer time periods. While it is impossible to conduct a 90 + yr preservation experiment, it is reasonable to expect that formalin fixation would have no isotopic effect since formalin itself does not contain nitrogen, nor does it alter bonds associated with individual amino acids (Ogawa et al. 2013).

Present-day forage fish samples from Lake Michigan were collected in April–May 2015 by USGS and from Lake Superior in October 2014 by University of Minnesota, Duluth, using bottom trawl sampling. Present-day species sampled included bloater and alewife in Lake Michigan and bloater, kiyi, alewife, and rainbow smelt in Lake Superior.

All specimens were frozen until processed. A dorsal muscle plug was dried in a drying oven at 48°C and ground to a powder. Three individual fish were analyzed for each species–lake–period combination.

Amino acid-specific stable isotope analysis was conducted at Japan Agency for Marine-Earth Science and Technology via the methods described by Chikaraishi et al. (2015). 12 N HCl hydrolysis at 110°C (overnight, >12 h) was used to prepare the samples for the analysis, and *n*-hexane/dichloromethane (3/2, v/v) was used to wash the hydrolysate of hydrophobic constituents following hydrolysis. Derivatization of the samples was conducted using thionyl chloride/2-propanol (1/4, v/v) at 110°C for 2 h followed by pivaloyl chloride/dichloromethane (1/4, v/v) at 110°C for 2 h. *n*-Hexane/dichloromethane (3/2, v/v) was then used to extract the amino acid derivatives, and $\delta^{15}N$ values of amino acids were determined via GC/C/IRMS with a 6890N GC instrument (Agilent Technologies, Palo Alto, California, USA) coupled to a Delta^{plus}XP IRMS instrument interfaced through GC-C/TC III (Thermo Fisher Scientific, Bremen, Germany).

After every five to eight sample runs, reference mixtures of nine amino acids (alanine, glycine, leucine, norleucine, aspartic acid, methionine, glutamic acid, phenylalanine, and hydroxyproline) with known $\delta^{15}N$ values (ranging from −26.6‰ to +45.7‰, Indiana University, Bloomington, USA; SI Science, Sugito-machi, Japan) were analyzed to assess isotope measurement reproducibility. Before and after each reference mixture and sample chromatography run, three pulses of reference N_2 gas were also discharged into the IRMS for this purpose. The isotopic values of sample amino acids used to calculate trophic positions were expressed relative to air on scales normalized to the reference amino acids' known $\delta^{15}N$ values. Approximately 15% of samples were run in duplicate to check accuracy and precision. Reference mixture and sample (sizes of ≥1.0 nmol N) accuracy and precision were 0.0‰ (mean of Δ) and 0.4–0.6‰ (mean of 1σ), respectively. $\delta^{15}N$ values are reported for glutamic acid and phenylalanine. During HCl hydrolysis, the α-amino group of glutamine contributes to the $\delta^{15}N$ value calculated for glutamic acid and was affected by quantitative conversion of glutamine to glutamic acid.

Bulk stable nitrogen isotope analysis was conducted at the University of California—Davis Stable Isotope Facility using a Europa Hydra 20/20 continuous-flow isotope ratio mass spectrometer. Mean standard error for duplicate samples (N = 6) was 0.28‰. Bulk $\delta^{15}N$ was corrected for tissue preservation effects using correction factors for fish which were formalin-fixed and transferred to ethanol (+0.44‰ for $\delta^{15}N$; Schmidt et al. 2009).

Amino acid-specific trophic position of each sample was calculated using the $\delta^{15}N$ values of glutamic acid and phenylalanine, where β represents the difference in the $\delta^{15}N$ value of glutamic acid and phenylalanine in primary producers and trophic discrimination factor (TDF) represents the $\delta^{15}N$ offset between glutamic acid and phenylalanine enrichment ($\Delta\delta^{15}N_{Glu} - \Delta\delta^{15}N_{Phe}$): $TP_{Glu/Phe} = (\delta_{15}N_{Glu} - \delta^{15}N_{Phe} - \beta)/TDF + 1$. We assumed $\beta = 3.4‰$, and used a general TDF value of 7.6‰, as proposed by Chikaraishi et al. (2009) for

aquatic systems. All statistical analyses were conducted using the statistical programming language R (R Core Team 2014). Differences among historical deepwater coregonine and present-day forage fish trophic position were examined using two-way ANOVA. Correlation analysis was used to compare historical deepwater coregonine trophic positions and bulk $\delta^{15}N$ values between Lake Michigan and Lake Superior. Two-sample *t*-tests were used to compare trophic positions of Lake Michigan and Lake Superior forage fishes between historic and present-day periods.

Results

Across both Great Lakes and historical and present-day periods, amino acid-specific trophic position varied significantly among species, lakes, and time periods. There was also a weak species × historical to present-day time period interaction, suggesting that the magnitude of the temporal shift differed among species (ANOVA; Species: $F_{8,34} = 35.7$, $P < 0.001$; Lake: $F_{1,34} = 9.4$, $P = 0.004$; Period: $F_{1,34} = 144$, $P < 0.001$; Species × Lake: $F_{4,34} = 1.6$, $P = 0.2$; Species × Period: $F_{1,34} = 5.2$, $P = 0.029$; Lake × Period: $F_{1,34} = 0.1$, $P = 0.74$; Table 1). The lake effect was not significant when the historic and present-day periods were analyzed separately, which suggests that the lake effect in the overall model is due to differences in trophic position between the two time periods (Historic ANOVA; Species: $F_{6,24} = 35.6$, $P < 0.001$; Lake: $F_{1,24} = 0.45$, $P = 0.51$; Species × Lake: $F_{4,24} = 0.8$, $P = 0.54$; Present ANOVA; Species: $F_{3,10} = 29.8$, $P < 0.001$; Lake: $F_{1,10} = 0.1$, $P = 0.75$).

Comparing historical and present-day periods, there was a significant downward shift in forage fish trophic position (*t*-test, Michigan: $t = 3.68$, df = 25, $P = 0.001$; Superior: $t = 3.97$, df = 19.1, $P < 0.001$; All: $t = 4.98$, df = 32.7, $P < 0.001$; Fig. 1). At the species level, Lake Michigan bloater, Lake Superior bloater, and Lake Superior kiyi (the only species–lake combinations available for both historical and present-day periods) trophic positions were significantly lower in the present-day period (*t*-tests assuming unequal variance, Lake Michigan bloater: $t = 11.44$, df = 2, $P = 0.008$; Lake Superior bloater: $t = 6.39$, df = 3, $P = 0.008$; Lake Superior kiyi: $t = 15.50$, df = 3, $P < 0.001$).

Table 1. ANOVA results comparing historic (1922–1923) and present-day (2014–2015) prey fish communities in Lake Michigan and Lake Superior.

ANOVA factor	df	*F* or *t*	*P*
Species	8,34	35.7	<0.001***
Lake	1,34	9.4	0.004**
Period	1,34	114	<0.001***
Species × lake	4,34	1.6	0.2
Species × period	1,34	5.2	0.029*

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Our sampling of present-day Lake Michigan produced few forage fish species compared to historical time periods and contemporary sampling in Lake Superior. Present-day Lake Michigan exhibited less overall variability in amino acid-specific trophic positions compared to other lake–period combinations, and this result was not simply due to differences in sample size (Fig. 1; historic Lake Superior CV = 7.28, N = 15; historic Lake Michigan CV = 7.49, N = 21; present-day Lake Superior CV = 7.05, N = 9; present-day Lake Michigan CV = 2.17, N = 6).

For the historical time period, there was a strong positive correlation between trophic positions of the deepwater coregonine species in the two lakes (Pearson's correlation; $t = 6.94$, df = 3, $r = 0.97$, $P = 0.006$; Fig. 2a). In contrast, there was no relationship between the two lakes for deepwater coregonine bulk $\delta^{15}N$ (Pearson's correlation: $t = 0.96$, df = 3, $r = 0.49$, $P = 0.41$; Fig. 2b).

Discussion

The Laurentian Great Lakes have undergone a multitude of ecological changes in response to anthropogenic activity. Using amino acid-specific stable isotope analysis of museum-preserved and present-day Great Lakes forage fishes, we describe declines in forage fish trophic position over the past century, coincident with native species losses and changes to the pelagic community. Our analysis also revealed distinct and clear trophic niche partitioning among deepwater coregonines during historical time periods. This trophic niche partitioning among deepwater coregonines seems to have persisted until the present-day in Lake Superior. In contrast, present-day Lake Michigan, which has undergone deeper impacts and has lost more deepwater coregonine diversity, exhibits virtually no niche partitioning among the remaining

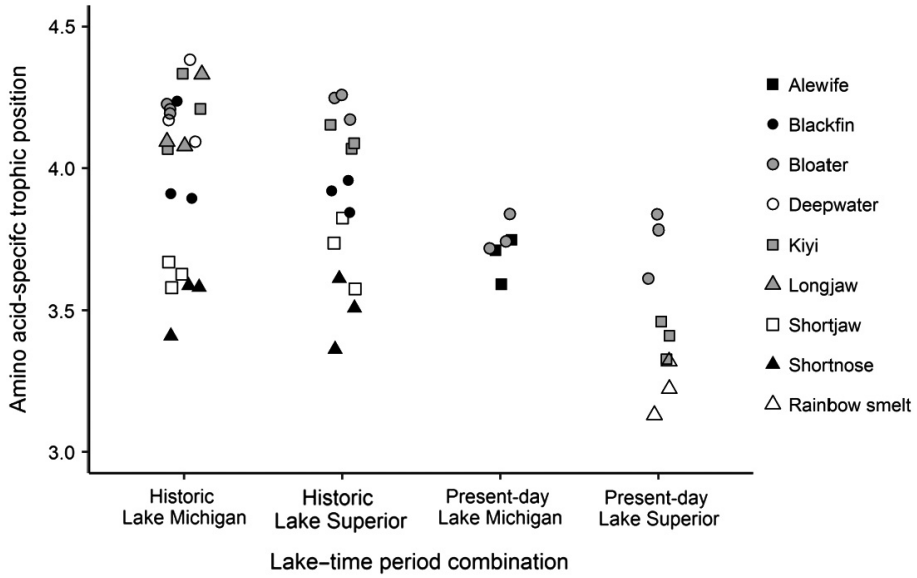

Fig. 1. Historic (1922–1923) and present-day (2014–2015) amino acid-specific trophic positions of Lake Michigan and Lake Superior forage fishes. N = 3 for each species–lake–period combination. Alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), kiyi (*Coregonus kiyi*), rainbow smelt (*Osmerus mordax*), deepwater (*Coregonus johannae*), longjaw (*Coregonus alpenae*), blackfin (*Coregonus nigripinnis*), shortjaw (*Coregonus zenithicus*), and shortnose ciscoes (*Coregonus reighardi*).

sampled deepwater coregonines. Present-day Lake Michigan can be described as exhibiting trophic compression compared to Lake Superior or historic conditions in Lake Michigan (Fig. 1).

Several long-term studies have described shifts in consumer trophic position with ecological change. For example, Hebert et al. (2009) observed declines in the trophic position of Lake Huron herring gulls from 1981 to 2005, attributing the shift to reduction in prey fish populations. Similarly, Gibson (2011) found the $\delta^{15}N$ values of macaques in Singapore to have decreased over the past century, reflective of habitat and biodiversity loss. Shifts in trophic position have been documented for various taxa and ecosystem types, differing in the direction of the shifts and contributing factors (Becker and Beissinger 2006, Norris et al. 2007, Britton et al. 2010, Rennie et al. 2011, Edelist et al. 2013). Loss of apex predators and non-native species introductions have both been shown to coincide with decreases in trophic position (Pauly et al. 1998, Vander Zanden et al. 1999, Byrnes et al. 2007). In our study, both lakes have experienced species introductions and native species declines or extirpation, such that changes in the prey fish community between the two periods could be contributing to the downward shift in trophic position.

In our study, a downward shift in trophic position of deepwater coregonines was observed in both Lake Michigan and Lake Superior, despite greater anthropogenic impact and nutrient loading in Lake Michigan. There are a multitude of factors which could potentially contribute to a downward trophic shift for this trophic group. Because our samples were from periods nearly 100 yr apart and because of the vast ecological changes which occurred over this time period, we cannot deduce the precise cause of the observed trophic shifts. In addition to non-native fish introductions and native fish species declines as described above, eutrophication or changes in zooplankton trophic ecology are possible factors. Another possibility that could decrease the trophic position of deepwater coregonines is a shortening of the zooplankton food web, leading to a reduction in the trophic position of invertebrates such as *Mysis* that composed a large proportion of prey fish diets. The historical gut content *Mysis* from Lake Michigan had a trophic position of 2.9, while mean trophic position of Lake Superior *Mysis* reported in Kruger et al. (2016) was 2.7. We did

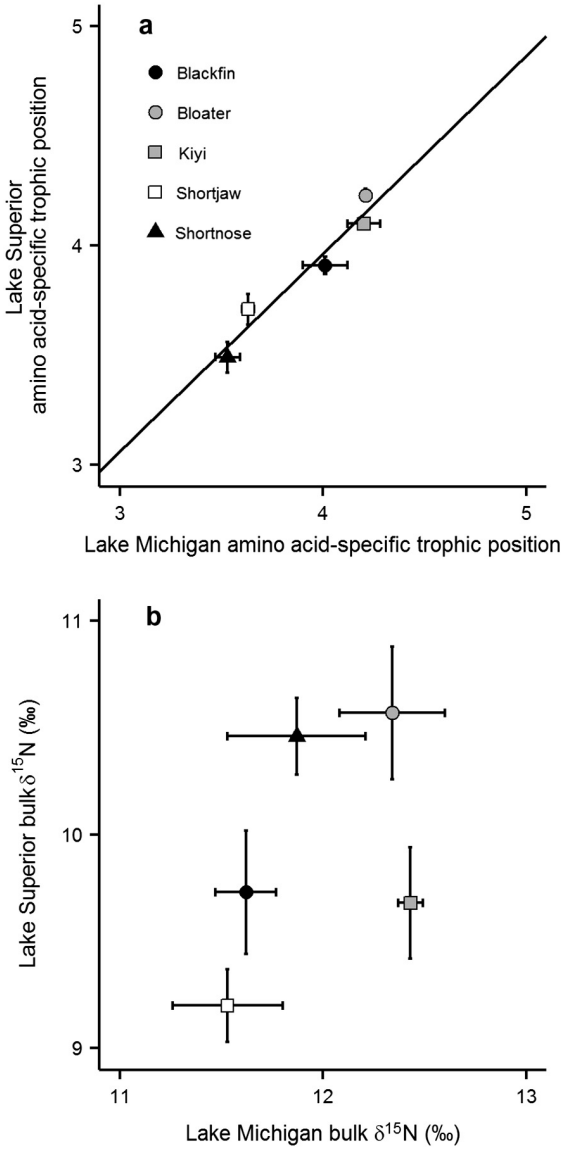

Fig. 2. Amino acid-specific trophic position was conserved between deepwater coregonines (bloater (*Coregonus hoyi*), kiyi (*Coregonus kiyi*), blackfin (*Coregonus nigripinnis*), shortjaw (*Coregonus zenithicus*), and shortnose (*Coregonus reighardi*) ciscoes) in Lake Michigan and Lake Superior from the historical study period (1922–1923; Pearson's correlation $r = 0.97$; a). There was no relationship using the bulk tissue stable isotopes (b). Error bars ± 1 SE.

not estimate trophic position of present-day Lake Michigan *Mysis*, but if similar to that of Lake Superior, it suggests that *Mysis* trophic position has not changed much.

In Lake Michigan, the coefficient of variation for trophic position of present-day forage fishes (bloater and alewife) was small compared to that of the other lake–time period combinations. We note that only two forage fish species were collected, which is reflective of the depauperate state of the current forage fish community. While the composition of species sampled in Lake Michigan is dramatically different between the two time periods, the species that were sampled represent the dominant prey fish species present in the two time periods. These changes in forage fish species composition prevent us from comparing individual species across the two time periods, though we can still consider trophic changes in the prey fish community as a whole. Lake Superior has been affected to a lesser degree by anthropogenic influence, and though the trophic positions of Lake Superior bloater and kiyi appear to have decreased similarly to those of the present-day Lake Michigan forage fishes, the coefficient of variation for present-day forage fish trophic positions was similar to that of the historical deepwater coregonines in both lakes. Notably, non-native rainbow smelt had the lowest trophic position of the forage fishes sampled, partially contributing to the overall downward trophic position shift.

Changing invertebrate communities may also be a factor in the observed changes in trophic niche partitioning. *Diporeia*, an important food source for deepwater coregonines (Koelz 1929), have not declined in Lake Superior, while in Lake Michigan *Diporeia* have undergone sharp declines (Nalepa et al. 2009). *Diporeia* consume primarily phytoplankton detritus and benthic algae (Sierszen et al. 2006). Kruger et al. (2016) reported trophic position of *Diporeia* to be 2.4 and *Mysis* to be 2.7. Given this difference, the trophic compression in Lake Michigan relative to Lake Superior could be the result of the sharp decline in *Diporeia* in Lake Michigan (Nalepa et al. 2009), which reduced the breadth of the prey base, and thus reduces the potential for niche partitioning at higher trophic levels. The overlapping trophic positions of present-day Lake Michigan bloater and alewife suggest that these fishes may be competing for similar, diminishing resources.

This similarity in trophic position among present-day Lake Michigan pelagic forage fishes is in stark contrast to that of the historical period. Trophic position differed among species in both

Great Lakes in the historical period, thereby extending past work describing historical niche partitioning among deepwater coregonines (Schmidt et al. 2011). Amino acid-specific trophic position and gut content-derived *Mysis* sampled herein (Appendix S1: Table S1) suggest that the historical deepwater coregonines differed in their consumption of *Mysis*, *Diporeia*, and other zooplankton. They also differed in their depth preferences and diel migrations (Koelz 1929, Hondorp et al. 2005, Bunnell et al. 2015). This variability in resource use and life-history presumably facilitated the linking of primary production to higher order, pelagic consumers (Bunnell et al. 2015, Eshenroder et al. 2016). The subsequent loss of deepwater coregonine diversity in the Great Lakes was accompanied by the loss of these trophic pathways, weakening the system's capacity for energy and nutrient transfer.

Trophic position of historical deepwater coregonines was strongly conserved across Lake Michigan and Lake Superior (Fig. 2a). We might expect to see similar trophic niches because the two Great Lakes historically had yet to be altered by anthropogenic stressors, and shared similar communities and trophic states (Devictor et al. 2010, Barbiero et al. 2012). Interestingly, across-lake similarities in diets and habitat use have also been observed in morphs of the European whitefish (*Coregonus lavaretus*) in Norway (Ostbye et al. 2006).

This observation of similarities in trophic position across the two lakes also highlights the advantages of the amino acid-specific approach for detecting ecological patterns. Differences in trophic niche partitioning across sites or over time cannot be reliably assessed without an isotopic baseline (Fig. 2b). It can be particularly difficult to provide an isotopic baseline when working with historical samples using bulk tissue stable isotope analysis (Cabana and Rasmussen 1996, Schmidt et al. 2009, 2011). Using bulk stable isotopes, Schmidt et al. (2009, 2011) found coregonine species to have distinct trophic niches, but found no evidence for trophic declines or compression, as reported here. The amino acid-specific approach can allow reconstruction of historical niche partitioning and elucidate patterns that may not be evident using bulk stable isotope methods.

Finally, trophic position estimated by amino acid-specific stable isotope analysis provides insights into the puzzling taxonomy of the deepwater *Coregonus* species. *Coregonus reighardi* and *Coregonus zenithicus*, deemed a single taxon by Todd and Smith (1980), both had low amino acid-specific trophic position historically relative to other deepwater coregonines. This finding highlights the potential for this approach to reveal the relationship between morphology and a measure of ecological function. In contrast, Todd et al. (1981) suggest that *Coregonus zenithicus* and *Coregonus alpenae* are synonymous genetically, and many researchers now treat the two species as a single taxon. Our data place them on opposite ends of the trophic spectrum (Fig. 1). However, it should be noted that Great Lakes deepwater coregonines differ genetically (and often phenotypically, behaviorally, and morphologically) depending on their location within a lake (Turgeon and Bernatchez 2003). The capacity of deepwater coregonines to defy species concepts reminds us that ecological diversity is not confined to taxonomic classification alone.

Conclusions

Food webs play a central role in structuring ecological communities (McCann 2007, Estes et al. 2011). Perhaps not surprisingly, consideration of food webs has emerged as an important element of ecosystem management and ecological restoration over the past decade (Vander Zanden et al. 2016). Yet ecological restoration is often carried out with little knowledge of historical conditions or food web relationships. While, in many cases, it is impossible to infer historical food web relationships, stable isotope analysis of museum specimens can offer insights into historical food webs. In this study, amino acid-specific stable nitrogen isotope analysis revealed historical food web structure and niche partitioning among members of a now-decimated species flock from nearly 100 yr ago. While recognizing that restoring a trophically diverse forage fish base is only one of many factors to consider in ongoing ecosystem rehabilitation efforts, our results support that bringing back a trophically diverse prey base may contribute to ecological restoration objectives and facilitate energy flow to higher trophic levels.

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